THE ANTENNÆ OF DIPTERA; A STUDY IN PHYLOGENY.

S. W. WILLISTON,
CHICAGO, ILL.

No classification of the order Diptera is, on the whole, satisfactory. Four or five more or less elaborate schemes have been proposed by various writers in the past, but none has received general endorsement by students of the order. Scarcely any two writers agree as to the relationships of the larger part of the families, nor as to the value of many of their distinguishing characters. And this unsatisfactory condition is doubtless largely due to our failure to differentiate between homoplastic or convergent resemblances and genetic characters. As in all other large groups of animals there have been many phyletic lines of descent, many parallel adaptations to like environments, and these adaptive characters, here as elsewhere, have been, too often, used as fundamental classificational characters. Of past writers Osten Sacken was, I believe, most appreciative of such accidental resemblances; but even he often mistook adaptive for hereditary characters I am convinced.

The attainment of like characters by evolution by no means necessarily implies common ancestry. One would not think of uniting all flies having two-jointed palpi in one group, nor all those having a club-shaped abdomen in one suborder. But there are many other characters, less conspicuous ones, which have been used for such purposes, whose origins have been due to adaptations; and it will be long before we have thoroughly learned to distinguish them. New characters acquired in different phyla are seldom, perhaps never, exactly alike, though there may often exist the most curious resemblances, due doubtless to similar determining causes, or to orthogenesis, if there be such a thing. To paleontology we are indebted for the formulation, at least, of the apparent law that evolution is irreversible — that organs once functionally lost are never regained. There may be exceptions to this rule, but, so far, the history of past life seems

to teach that there are not. A fly with two-jointed palpi, for instance, could not have been ancestral to one with four joints in these organs.

Of all the organs of diptera, the antennæ, it seems to me, have received less critical comparative study than any others, and I believe that there is a fertile field here for fruitful phylogenetic studies. The differentiation between the nematocerous and brachycerous flies was, for a long while, based almost exclusively upon the structure of these organs; until it was conclusively shown that, by themselves, they have little classificational value. The antennæ, for instance, of *Bibio* are so nearly identical with those of *Xylophagus* that they might be interchanged without affecting generic characters, even as the wings and palpi of the phorids might be interchanged with some of the scatopsines without affecting generic characters. It was doubtless because of this primary division long ago by Latreille and Macquart into "many-jointed" and "three-jointed" antennæ that a misconception still exists among many as to the real structure of these organs. There are very few three-jointed antennæ among diptera, and even these will usually show, under high magnification, vestiges of additional joints. The great majority of existing diptera have five or six joints in their antennæ, and this majority includes the whole of the Cyclorrhapha, with but few exceptions. The fallacy has been in considering the antennal style or "arista" as an outgrowth or addition to the real antenna, whereas it is of course merely the specialized and more or less attenuated distal (?) part of the flagellum, showing all stages of attenuation and abbreviation; and it is yet to be shown that the arista is quite homologous in all diptera.

In the following table I have condensed the results of considerable observation and research on the structure of the antennæ in the different families of flies. It is of course impossible for one to examine critically all the genera of diptera, and the published data are yet, in many cases, inexact, and this inexactness is especially apparent when it comes to the detection of vestigial or minute joints. I have found under critical examination not a few instances of minute joints which have been neglected by systematists in general. Such a study as the present one must

take into account all vestiges and aborted organs if one would arrive at precise results. The Phoridæ, for instance, have been shown by Brues and others to possess two scape joints, though but one has usually been ascribed to them. And this will probably be found to be true of all the other so-called two-jointed antennæ, such as those of certain cyrtids, empidids and dolichopodids, under close examination. I have arranged the families in the following list not quite in the supposed order of their relationships, in order to bring out more clearly the antennal structure. I have also for the few families showing archaic forms given the extremes in parenthesis, with the "normal" or usual numbers in the regular column.

Tipulidæ (6–39)	12–16	Acanthomeridæ	10
Cecidomyidæ (6–36)	12–16	Tabanidæ	6–10
Psychodidæ	12–16	Leptinæ	3–8
Mycetophilidæ	12–16	Nemestrinidæ	5–6
Pachyneurinæ	12–16	Mydaidæ	4–5
Rhyphidæ	12–16	Apioceridæ	3–5
Dixidæ	15	Asilidæ	3–5
Culicidæ	14–15	Therevidæ	3–5
Blepharoceridæ	9–15	Scenopinidæ	3
Chiromomidæ	6–15	Bombyliidæ	3–5
Orphnephilidæ	11–12	Dolichopodidæ	4–5
Bibioninæ	8–12	Empididæ	3–5
Scatopsinæ	9–10	Lonchopteridæ	6
Simuliidæ	10	Phoridæ	6
Xylophaginæ (13–30)	9–10	Cyclorrhapha	5–6
Stratiomyidæ	7–10		

In this list we are at once struck with the predominance of five groups having the maximum normal number of sixteen, fifteen, ten, six and five. And I venture to suggest that these five groups represent, in the main, long since divergent phyla of diptera. Not invariably of course, because coincidences may and often do occur in the different lines of descent. There are quite a number, it is seen, having the maximum number of fifteen. Possibly these may represent one common branch from the sixteen-jointed antennæ, possibly several. But, in none of these groups, unless it be the fifteen jointed, and of course the primitive Tipulidæ and

Cecidomyidæ, do I believe that we shall often, if ever, find vestigial joints additional to the maximum — simply for the reason that the loss of additional joints has been so far back in geological history that vestiges have wholly disappeared.

If the law of irreversibility in evolution be true, then it is apparent that no fly has regained the use of a joint of the antennæ once functionally lost. The question at once becomes important: What was the original number of antennal joints in the Diptera? If we could only be assured of the origin of the order from the main insect stem, we might, perhaps, answer this question with satisfaction. But, since we cannot we are forced to depend upon the internal evidence presented by the diptera themselves. May we assume that this primitive number was sixteen, the number so conspicuous in the table? Or was it thirty-nine (or more) a number known in a single species of diptera? I have assumed that the evolution of the dipterous antenna has been by the reduction of the number of segments, and never by accretion. And I believe that this assumption is justified, though the matter is perhaps open to debate. There are very few forms of diptera known possessing more than sixteen antennal joints. Some species of *Pachyrhina* and of the nearly allied *Nephrotoma* among the Tipulidæ have nineteen joints in the male, fifteen or sixteen in the female. The genus *Ctedonia*, of the same family, from Chile, has twenty-two or twenty-four joints in the flagellum of the females of two species, fifteen in that of a third. . . . The very closely related *Cerozodia*, from Australia and New Zealand, with two species, known only in the males, has thirty-two and thirty-seven flagellar joints respectively, the largest number hitherto discovered in any dipteron. As Osten Sacken truly said: "The close affinity between *Cerozodia* and *Ctedonia* affords a new instance of the curious relationships between the Australian and New Zealand fauna and that of Chile [South America]; a relationship exemplified in abnormal forms, apparent survivals of past ages, of which we already have" many other equally remarkable instances in all branches of animal life, recent and fossil. And precisely similar is the relationship between *Tanyderus pictus*, of the same family, from Chile, with twenty-five antennal joints, and *T. ornatissimus* from Amboina, with twenty-two joints.

Gynoplistia, another tipulid genus, from Australia, New Zealand, New Guinea and Celebes, with numerous species, has from sixteen to twenty antennal joints, branched like those of *Cerozodia*. Are these forms really survivals of primitive types? I do not think that we are permitted to doubt it. Their habitats and distribution alone indicate that, and the fact that three of the few known forms of diptera with multiarticulate antennæ are known only from the Miocene is also corroborative. *Magachile*, perhaps identical with *Protoplasa*, is one of these amber forms.

Among the Cecidomyidæ we have a few forms with multiarticulate antennae, as many as thirty-six in the males of some *Hormomyiæ* with a maximum of twenty-four in the females. The only other forms with abnormal multiarticulate antennæ that I can discover in the literature, are *Rhachicerus*, with from twenty to thirty joints, *Chrysthemis*, an amber genus with twenty-three joints; and *Electra*, also from the amber, with thirteen joints, all belonging to the xylophagid "Brachycera," having a normal maximum number of ten joints. The fact that some of these examples have a larger number of joints in the male antenna than in the female, may seem to indicate that the increased number is an acquired secondary sexual character, and that the female antenna is nearer the primitive number. But, why may we not assume that the diminished number in the female is the real acquired sexual character, and not the increased number in the male? Certainly this *must* be the case with such forms as *Tanypus* and its allies among the Chironomidæ, *Micromyza* and others of the Cecidomyidæ. From the frequent occurrence of sexual variation in these apparently primitive forms, I think it is probable that the early diptera all had fewer antennal joints in the females than in the males. I am confident that we are safe in accepting at least thirty-nine as the original and primitive antennal number among diptera; safe in the belief that the evolution of the dipterous antenna has always been by reduction from this primitive number, and never by the reacquirement of joints once lost.

Just how the loss of antennal joints has occurred is not always clear. It may be assumed that it has been by the loss of distal segments, but this is certainly not always the case, especially when

these distal joints have been highly specialized. The scape is perhaps never entirely reduced. The genus *Chionea*, a wingless tipulid, has the conical third antennal joint terminating in a slender, three-jointed style, a structure very much like that of the Nemestrinidæ, for instance. Do these joints represent the first four of the flagellum? Osten Sacken thinks that the reduced number of twelve joints in *Toxorhina*, belonging in a group having the normal number of sixteen, is due to the coalescence of the basal joints of the flagellum. The stratiomyid genus *Chrysochlora*, as one of numerous instances, with the normal number of flagellar joints, has the last or eighth specialized into a slender arista. Is this arista homologous with the arista of the housefly, for instance, where it is serially the fifth or sixth? The defect of the Comstock-Needham system of venation nomenclature is the assumption that the disappearance of veins has always been due to coalescence, whereas we positively know that in many cases it has been due to their loss without coalescence. Has the reduction of the flagellum been the result of the close fusion of segments, or the absolute loss of proximal ones; or has the arista been variously and repeatedly produced by the attenuation of the last segment or segments, whichever they happen to be? I believe that the arista has usually resulted from the former method and that it generally is homologous. It is quite clear, however, that the diminution in the number of homologous or homonymous joints has often been due to the loss of distal segments, whatever may have been the case with heteronymous forms; and the proof of this is apparent in the oftentimes vestigial condition of the terminal joints. The subject, however, is one worthy of investigation, and may throw light on the relationships of many of the diptera.

Sixteen antennal joints seem to be the primitive normal number of the modern Nemocera, a number acquired so long ago that very few examples yet remain of the more primitive condition. Do they indicate a single phylum? It seems doubtful. The forms with multiarticulate antennæ not only belong in the three chief subdivisions of the Tipulidæ, but are also found among the Cecidomyidæ, which would seem to indicate that the number sixteen had been acquired independently in different lines of de-

scent — that family or subfamily differentiation had occurred before the final reduction took place. It is also curious to observe that the minimum number of antennal joints in the Tipulidæ, Cecidomyidæ and Chiromomidæ is six, precisely the maximum number of the Cyclorrhapha.

In living forms the maximum and very common number of flagellar joints among the Brachycera, with the exception of *Rhachicerus*, is eight, found so frequently in the Xylophagidæ, Stratiomyidæ, Tabanidæ and Acanthomeridæ. Is this coincidence of phylogenetic significance? I feel quite sure that it is. I think that no one can dispute the relationships between *Rhachicerus* and the Xylophaginæ. Is *Rhachicerus* a belated survival of the xylophagid ancestors? If so, the phylum must have branched off long ago from the Tipulidæ (the venation excludes all other families, save the Rhyphidæ), before the antennæ had become reduced below thirty segments. One thing at least seems very evident, the Rhyphidæ are not the nearest related to the Xylophagidæ of the nematocerous families, as is usually believed. The Brachycera had their origin evidently directly from the ancestral Tipulidæ.

Likewise all of the five-jointed families would seem to be excluded from ancestral relationship with the six-jointed forms, and especially the Cyclorrhapha, though possibly the reduction has occurred since divergence.

While the antennæ, taken separately, may offer suggestions as to phylogenies of the dipterous families, and while they may absolutely veto such theories as imply reversion, they can settle none by themselves; they must be correlated with all the other organs of the body, and must harmonize with theories derived from other organs. I offer, nevertheless, the foregoing suggestions, in the possibility or probability that they may find corroboration

Secondary sexual characters are transmitted by heredity to the other sex, unless inhibited by sexual utility, or, possibly, sexual selection. It was for the casual statement of this law to a class in paleontology that I have recently been made the victim of a sensational press. The primitive eyes of diptera were doubtless separated by the front equally in both sexes. As a sexual character the eyes have become contiguous above the antennæ,

almost invariably a male character. There is evidently a sexual use for this greater development of the eyes in the male that has preserved the character with but little tendency to transmission to the female. It has, however, been transmitted to the female in some instances, and there are a very few forms in which the female has acquired the character in advance of the male. Examples of the former may be found among the Cyrtidæ, but a better one is that of *Systropus* of the Bombyliidæ, with contiguous eyes in both sexes, while the very nearly related *Dolichomyia* has the female eyes separated by the front. It was for the contiguity of the eyes in the male that Osten Sacken twenty-five years ago proposed the convenient term "holoptic," the antithesis of which, "dichoptic," was suggested by me a little later. But Osten Sacken's meaning of the term has been somewhat misunderstood. He gives as a definition of his Nemocera vera the nonholopticism of the eyes, while it is well known that some forms in this group do have contiguous eyes. But Osten Sacken really meant sexual holopticism, not simply contiguity of the eyes on the front. It remains to be proven that sexual holopticism does not really occur among these families of flies. If so, however, the occurrence must be extremely rare.

The primitive dipteron must have had eight fully developed longitudinal veins (including the auxiliary vein), with the second, third, fourth and fifth furcate; and a complete discal cell. The head was rather small, with the compound eyes separated equally by the front in both sexes. The ocelli were functional, and the maxillary palpi had four freely articulated joints; the labial palpi had probably already disappeared, though Wesche thinks differently. There were at least thirty-nine antennal joints in the male. The prothorax, mesothorax and metathorax were imperfectly fused, and the metanotum was visible from above. The abdomen had nine functional segments; the body was without differentiated bristles; and the tarsi had membranous pulvilli and empodia. The primitive flies were of moderate or small size, and probably crepuscular in habit, or at least denizens of shady forests.

Of modern diptera the Tipulidæ approach most nearly this hypothetical ancestor, but they have become specialized by a general increase in size, by the almost complete loss of the

ocelli; by the loss of the pulvilli; and the loss of the branch of the third vein, save among some of the Ptychopterinæ. The Rhyphidæ come next, but they have acquired holoptic eyes in some forms. Of the other families, the Psychodidæ and Culicidæ are perhaps the nearest allied to the original type, notwithstanding the occasional occurrence of multiarticulate antennæ among the Cecidomyidæ. The Culicidæ evidently represent an old type geologically, recrudescent in later times. Their fixed venation and antennal structure could only have come from long inheritance in a phylum which has not yet reached decadence. The blood-sucking habit of the mosquitoes is doubtless a rather recently acquired one, probably since the great development of the warm-blooded animals, as is evidenced by the almost innumerable sexual modifications of the palpi, modifications seldom found among the other families of Nemocera. The mosquitoes doubtless arose from the Corethrinæ, now decidedly on the wane. Every family, save the Tipulidæ, is I believe, absolutely excluded from immediate genetic relations with the Brachycera, because of the venation and the antennæ. I am, upon the whole, inclined to the belief that Osten Sacken was right in insisting upon the taxonomic importance of the Nemocera, as one of the chief phyla of diptera.